Sexual Conflict and Choice in a Phoretic Fly, *Borborillus frigipennis* (Sphaeroceridae)

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ABSTRACT   In the phoretic sphaerocerid *Borborillus frigipennis*, male size is important to sexual success. Large males prevent smaller rivals from approaching mates and have a higher rate of copulation per female encounter. The latter may be due to female preference for larger mates rather than male ability to force females into submission. Smaller males abandon beetles bearing formidable rivals.

MALES PRODUCE small, cheap gametes, and their reproductive success is generally limited by access to females. Such access is often influenced by competition from sexual rivals. At its most obvious, the resulting intrasexual selection has produced Diptera with spined maxillary palps, curious antlers, and stalk-eyes (Wallace 1869, Bristowe 1924, McAlpine 1975, 1979, Spieth 1981). But the absence of extravagant features does not mean an absence of conflict (consider the struggles of the yellow dung fly, *Scatophaga stercoraria*, [Parker 1970, Borgia 1981a], or male-male interaction in the Caribbean fruit fly, *Anastrepha suspensa*, [Burk 1983]). Females form large gametes, and offspring numbers are limited by production of ova, not by sexual encounters (Trivers 1972). However, there is a growing body of circumstantial evidence that females can increase offspring quality by choosing for them the genetically best father (Thornhill 1980). At its strongest, such intersexual selection pressures lead to complex, colorful male advertisement and "sales-resistant" females, typified by the lekking Tephritidae (Burk 1981).

The phoretic sphaerocerid fly *Borborillus frigipennis* has certain advantages for the study of reproductive conflict and choice (Fig. 1). *B. frigipennis* oviposits in the fecal stores of scarabs. To reach these caches it rides beetles as they burrow, remains with them underground for up to a day or more, and will then sometimes continue to grip the host as it flies away (Sivinski 1983a). Its mating sites, the backs of scarabs, are easily transferred to the laboratory and are small enough to allow charting the sexual fates of individual flies upon them. The following is a description of *B. frigipennis*' sexual behavior and a discussion of what lies behind male reproductive success in the species.

Materials and Methods

Field observations were made and insects were obtained for study in Alachua County, Fla. To observe sexual interactions in the laboratory, *Phaneus* spp. dung beetles were placed singly in petri dishes (90 by 20 mm) along with damp sand and two male and one female *B. frigipennis*. Flies taken from the field were chosen solely on the criterion that they be recognizable as individuals due to size differences. After all three flies had mounted the beetle, homosexual and heterosexual activity was recorded and time spent off the host was determined with a stopwatch. Observation periods were 30 min long, but if coupling had not occurred in that time, they were occasionally extended in 15-min increments. A total of 20 arenas were observed. When observations were completed, the flies were preserved and their size was determined by measuring wing length with a stereoscope micrometer (because wings don't shrivel during preservation, they are standardly used to measure size in Diptera). Statistical tests used were chi-square (χ^2), t test (t), and correlation coefficient (r).

Results and Discussion

Description of Encounters Between Flies. The following observations are of flies both in the field and in the laboratory.

In both homo- and heterosexual interactions, a male climbs upon another fly's back, typically from the rear. Mounting is always followed by a brief flurry of agitation by the mounted insect. If a male is mounted, the pairing is usually terminated in ≤ 3 sec. It is not clear whether such homosexual encounters are aggressive or due to an inability to discriminate gender without contact. No uniquely agonistic behaviors were noted. If a female is mounted, the male may be dislodged during ≤ 10 sec of agitated female shaking. There is no obvious

Fig. 1. *B. frigipennis* upon the scarab *Canthon pilularius*. Flies are kleptoparasites of the beetles' buried dung caches and ride their hosts both underground and in the air. (Photo by J. E. Lloyd).

Fig. 2. Sizes of male *B. frigipennis* in relation to competitors (male wing length/competitor wing length) plotted against the proportion of the total recorded coupling time a male obtained. Dashed lines represent the point of equal size (vertical) and the point of equal coupling time (horizontal). Larger males account for significantly more couplings ($n = 40$, $\chi^2 = 36.76$, $P < 0.001$). Numbers within scattergram field represent the quantity of overlapping points at those coordinates.

premounting courtship. If the male remains mounted, the pair becomes relatively quiescent, only occasionally moving about or, very rarely, off the host. Couples disengage after an average of 151.8 sec ($n = 72$; range, 20–530; $s = 123.4$). Females spend up to 0.70 of the observation period coupled (mean $= 0.25$, $s = 0.21$). Mates break apart quickly.

B. frigipennis do not fly in copulo; the female's wings are clamped by the male's legs, and males make no effort to fly (unlike, for instance, the yellow dung fly, *S. stercoraria*, which lifts mates in flight [Borgia 1981a]). Rival males made one or more contacts with 50% of the mating pairs ($n = 56$). Competitors frequently mounted coupled males and attempted to engage female genitalia by stretching over and past the abdomen of the underneath rival. Alternatively, they attacked from the side and attempted to insinuate themselves between the coupled pair.

The initial activity associated with mating frequently attracts other males, so females may be mounted in rapid succession by multiple males. Rarely, females move to a beetle's sides or belly in apparent response to high levels of male encounters.

Size and Reproductive Success. Larger *B. frigipennis* are more successful in obtaining matings than are smaller competitors; bigger males engaged in 87% of all couplings. In 63% of the 20 arranged competitions, the larger male obtained all matings (Fig. 2; $\chi^2 = 39.56$, $P < 0.0001$). However, success is surprisingly independent of the de-
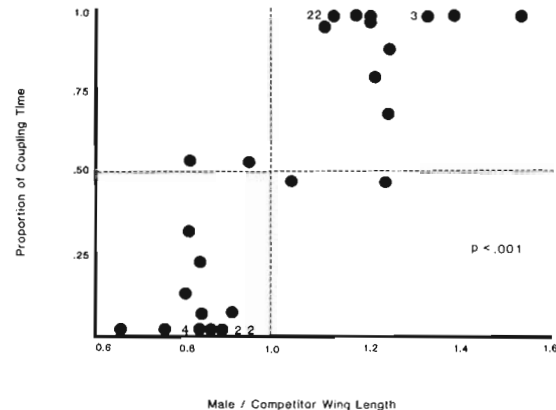
gree of size relative to competitors; that is, males slightly larger than neighboring males seem to enjoy a dominance similar to that of males that are much larger than their competitors (see Fig. 2; larger males' relative size is poorly correlated to percent coupling time, $r = -0.07$, $P > 0.25$). Larger males obtain more copulations in a number of animals (citations in Howard [1981], also Forrest [1980]), including some Diptera, e.g., *Scatophaga stercoraria*, (Borgia 1981a) and *Anastrepha suspensa* (Burk and Webb 1983); the relationship is not invariable, small males appear to copulate competitively in the bizarre drosophiloid, *Mystocinobia zelandica* (Holloway 1976). The success of larger males could be due to any or all of at least three factors: (i) large males are better able to subjugate uncooperative females; (ii) large males are able to control access to females; or (iii) females prefer to mate with large males.

Subjugation of Females. Two lines of evidence fail to support subjugation of reluctant mates as being of importance in the success of larger males. The first depends on male-female wing length (size) ratios to estimate male strength relative to its potential mate. When these ratios for larger males that obtained all matings are compared with smaller males that obtained no matings, there is a considerable overlap. That is, the larger males of male pairs that were relatively small compared with their mates obtained matings, although similarly sized smaller members of larger pairs failed to couple (38% of large, completely successful males were comparable in size relative to mates to 61% of smaller, utterly unsuccessful males). Another argument against larger males

being able to force unwilling females to copulate is the lack of correlation between successful male size–mate size and the proportion of mounting attempts resulting in coupling, a measure of a male's ability to sexually impose himself ($r = 0.14$, $n = 19$, $P = 0.29$).

Control of Access to Females. If larger males guard either females or the regions of beetles where females are apt to occupy, their greater success could be ascribed to greater mating opportunities. Heterosexual encounters are significantly more likely to be initiated by the larger male (64 versus 36% of 236 encounters, $t = 2.26$, $P < 0.025$). However, homosexual encounters are initiated by larger and smaller males with equal frequency (44 versus 50% of 262 encounters, $t = 0.90$, $P > 0.10$). The contrast between initiations of homo- and heterosexual encounters suggests that larger males have greater access to mates, i.e., smaller males are not less active than larger competitors, because they initiate homosexual encounters as frequently as large males, but they are kept from potential mates. Also indicative of large male control is equal access of large and small males to mating pairs, when the coupling male would presumably be unable to keep rivals from the area; there is no difference between the frequency of attempts by larger and smaller competitors ($t = 0.50$, $P > 0.25$), and relative male size is not correlated to security from attack ($r = 0.08$, $P > 0.25$). Large males in *S. stercoraria*, a dung-breeding fly, are also able to exclude smaller males from areas of high female density (Borgia 1981a).

Female Choice. Not only do smaller males initiate fewer heterosexual encounters, but their encounters are also less likely to result in coupling than are those of larger rivals. Larger males coupled in 37% of 163 encounters, and smaller males in only 9% of 97, suggesting that females prefer the larger of two rivals ($\chi^2 = 21.2$, $P < 0.0001$). A parsimonious explanation for such choice is that large fathers sire large sons, who will tend to have the reproductive advantage of restricting competitors' access to females. Benefits to offspring of both sexes might be gained by selection of bigger males, if size is an indicator of superior larval consumption rates, ability to avoid parasites, superior parental ability of the mother, etc. (e.g., Trivers [1972], Thornhill [1980]; *Drosophila melanogaster* larvae sired by males who are free to compete with other males or be chosen by females were more competitive than the offspring of unions arranged at random by an experimenter [Partridge 1980]).[2]

Male Discrimination of and Response to Competitors. Given variance in mating based on size, selection might favor males that assess competi-

tors' sizes and act on the information, perhaps by leaving an unsuitable host and searching for another. Big males spend less time off beetles (mean = 4% versus mean = 12% of observation period, $t = 14.67$, $P < 0.0005$), and "exiles" are particularly long where the difference in male size is greatest ($r = -0.26$, $n = 44$, $P = 0.04$).

In nature, smaller males may also leave scarabs. The comparison of *B. frigipennis* groups from the backs of flying and walking beetles suggests a nonrandom male abandonment of beetles. Aggregates of *B. frigipennis* on flying scarabs contain proportionately more females than those on walking beetles (flying, 60 males : 105 females, 64% female; walking, 578:624, 52% female, $P < 0.05$). Female biases are more likely due to male departures from groups that had previously been underground with the scarab host, rather than female colonization of recently emerged, soon to fly, beetles. There is no obvious opportunity for females to mount beetles in greater numbers than males, and because adult *Borborillus* do not dig well, females are unlikely to burrow to join underground aggregates. Sex ratios of walking and freshly buried spaerocerid groups are indistinguishable (i.e., males are not abandoning hosts at burial at a greater rate than are females [Sivinski 1983b]).

Male flight could be due to assessing superior competitors during days-long burials. If departing male *B. frigipennis* are experienced, then the distribution of male fly sizes might be different in walking and flying groups; older flying groups would be expected to have more similar-sized males than freshly formed walking groups. Such a change does occur. On flying beetles, mean male fly size is positively correlated to mean rival size ($r = 0.37$, $n = 28$, $P = 0.03$). There is no relationship between male fly size and mean competitor size, however, on the backs of walking scarabs ($r = 0.14$, $n = 74$, $P = 0.11$).

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[2] Male size is not heritable in *S. sterocoraria* (Borgia 1981a) nor in the ephydrid *Ephydra cinerea* (Collins 1980), but is highly so in *Musca domestica* (Bryant 1977) and *Drosophila simulans* (T. Geisel, personal communication). Nongenetic advantages to coupling with large males include predator defense (Borgia 1981b, Sivinski 1983) and ejaculate-borne nutrients (Gwynne 1983).

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